

FEEDING INTERRELATIONS OF NATIVE FISHES IN A SONORAN DESERT STREAM

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ABSTRACT.— Native fishes in Aravaipa Creek, Arizona, cropped foods proportional to abundance of those foods within the system. Ephemeropteran nymphs and adults comprised the major prey of 5 of 7 fishes (*Gila robusta*, *Meda fulgida*, *Rhinichthys osculus*, *Tiaroga cobitis*, and *Catostomus insignis*). The omnivorous *Agosia chrysogaster* ate almost as many nymphal mayflies as did the carnivores. *Pantosteus clarki* was herbivorous, taking animals only when they were abundant. When ephemeropterans decreased in abundance, a shift by some fish species occurred to other locally or seasonally abundant items. Other fishes continued to feed upon the same foods throughout the year. Abundance of invertebrates in Aravaipa Creek, coupled with marked spatial partitioning of habitat by fishes present, seemingly precluded severe interspecific interactions for food.

This paper provides information on foods and feeding of native fishes in Aravaipa Creek, south-central Arizona. That low-desert stream is unique because seven native fishes still coexist under natural conditions, scarcely disturbed by foreign influences. Only one nonnative species, the green sunfish (*Lepomis cyanellus* Rafinesque), has succeeded in maintaining a small population within the system. Indigenous kinds include two catostomids, *Catostomus insignis* Baird and Girard (Sonora sucker) and *Pantosteus clarki* (Baird and Girard) (desert sucker), and five cyprinids, *Agosia chrysogaster* Girard (longfin dace), *Gila robusta* Baird and Girard (round-tail chub), *Meda fulgida* Girard (spikedace), *Rhinichthys osculus* Girard (speckled dace), and *Tiaroga cobitis* Girard (loach minnow). We examined stomachs for all but the round-tail chub, which was too rare during our study period to allow adequate sampling. Data on its foods, provided by James E. Burton, Arizona State University (ASU), were derived from specimens taken between 1965 and 1977 and housed in the ASU Collection of Fishes.

In addition to determination of how and what was eaten, we explored the question of food availability. Estimates of population densities and biomasses of potential and actual foods were made (Schreiber 1978), and those data were examined to determine how

selective, or how opportunistic, the fishes were in their feeding.

Some additional information has appeared on Aravaipa Creek fishes. Barber and Minckley (1966) published an account of the ichthyofauna, and later reported on foods of spikedace relative to season, ontogenetic changes, and habitat (Barber and Minckley 1981). Barber et al. (1970) presented additional data on biology of the spikedace, Minckley and Barber (1971) presented information from Aravaipa Creek in their general treatment of the biology of the longfin dace, and Minckley (1973, 1981) and Deacon and Minckley (1974) discussed several aspects of the ecology of the stream's fishes.

STUDY AREA

Aravaipa Creek in Graham and Pinal Counties, Arizona, originates in Desert Grassland between the Pinaleno and Galiuro mountains and flows northwest then west for more than 100 km. Much of the stream bed is dry, with permanent water surfacing at about 1010 m above mean sea level near the town of Klondyke. The stream then enters Aravaipa Canyon to flow between high, stony cliffs for about 20 km. Below the gorge the stream passes through Sonoran Desert in an ever-widening valley to disappear into its gravelly bed. In periods of high runoff, it

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enters the San Pedro River at about 660 m. More details on topography, geology, and ecology of the region were given by Ross (1925), Simons (1964), Bruns and Minckley (1980), and Minckley (1981).

The creek consists of riffles (15 cm deep and 1.5 to 4 m wide) separated by broad (8 to 15 m) reaches of shallow runs (<6 cm deep) flowing over sand and gravel through often-braided channels. Moving bedload precludes formation of pools typical of streams with more stable bottoms. Pool habitats in Aravaipa Creek (0.5 to 1.5 m deep) are present only where canyon walls or other obstacles restrict width of the channel or deflect currents to induce undercutting. Discharge of Aravaipa Creek near its lower end averages about 0.85 m³/sec, with a range of essentially 0.0 to 570 m³/sec (U.S. Geological Survey, published periodically). Drought persisted during our study period, and mean discharge from January 1975 through January 1976 was 0.33 m³/sec; range was 0.05 to 3.1 m³/sec.

METHODS AND MATERIALS

Selection of a sampling site was dictated by abundance of fishes and a consistent presence of the maximum number of species. The

selected reach consisted of a 60 m, rubble-bottomed riffle, bounded up- and downstream by broad, shallow runs with sand-gravel bottoms. Pool habitat was provided where the creek was deflected from a canyon wall (Fig. 1). Widths of the flowing channel and depths of various habitats changed with discharge, but closely resembled average conditions given above.

Field collections of fishes, benthos, and drifting materials were made over five 2-day periods in 1975–1976 (Table 1). Fishes were sampled by seines 9.5 m long, with 6.4-mm mesh (bar measure) and electrofishing gear of 110 volts, 1200 watts, alternating current. The number of fish preserved was limited to a maximum of 5–10 individuals per species every 4 hours to avoid depletion of local stocks over a 28-hour period. Fish sampling was done downstream from the drift and benthos site. Fishes were preserved intact in 10 percent formalin; no regurgitation upon preservation (Starrett 1950) was noted.

Only subadult and adult individuals of each species were studied. Stomachs, or the digestive tract anterior to the first loop toward the head in fish with poorly defined stomachs (Catostomidae), were excised and



Fig. 1. Photograph of the sampling area in Aravaipa Creek, Graham County, Arizona, summer 1975.

TABLE 1. Occurrence of potential and actual food items in samples of benthos, drift, and fish stomachs from Aravaipa Creek, Arizona, on five sampling dates in 1975-1976. Left to right, dates of collections were 9-10 January, 18-19 April, 11-12 July, 24-25 October (1975) and 30-31 January (1976). The symbol "x" denotes presence of the item on a given date, "-" indicates its absence, and the symbol "+" denotes occurrence of items in stomachs of *Gila robusta*, based on data provided by James E. Burton (see text).

Items	Benthos	Drift	<i>Gila</i>	<i>Agosia</i>	<i>Meda</i>	<i>Rhin- ichthys</i>	<i>Tiaroga</i>	<i>Catos- tomus</i>	<i>Pant- osteus</i>
COLLEMBOLA									
Undetermined taxa	-----	XXXXX	-	-----	-----	-----	-----	-----	-----
Sminthuridae	-----	X----	-	-----	-----	-----	-----	-----	-----
EPHEMEROPTERA									
Undetermined adults	-----	XXXXX	-	---XX	-X-XX	-----	-----	-----	-----
Baetidae nymphs	XXXXX	XXXXX	+	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX
Tricorythidae nymphs	XXXXX	XXXXX	+	XXXXX	XXXXX	-X-XX	--XXX	XXXXX	--X-
Heptageniidae nymphs	X--X	X--X	-	X--X	X----	X----	-----	X-----	-----
Leptophlebiidae nymphs	XXXXX	XXXXX	+	XXXX-	XXXX-	-X---	-X---	-X---	-X--
Ephemerellidae nymphs	-X-X	-X---	-	-X---	-X---	-X---	-X---	-X---	-----
PLECOPTERA									
Capniidae adults	-----	X--X	-	X----	X----	-----	-----	X----	-----
Capniidae nymphs	X--XX	XX-XX	-	X--X	X--XX	X--X	X----	X-X-	X--X-
ODONATA									
Gomphidae nymphs	---XX	X-XX-	+	---X-	-----	-----	-----	X-XXX	-----
Libellulidae nymphs	---XX	-----	+	-----	-----	-----	-----	-----	-----
HEMIPTERA									
Undetermined terrestrial taxa	-----	XXXXX	-	-----	--XX-	-----	-----	-----	-----
Belostomatidae	-----	-----	+	-----	-----	-----	-----	-----	-----
Corixidae	---X	XXXXX	-	---X-	-X-	-----	-----	-----	-----
Mesoveliidae	-----	X-XXX	-	-----	-X--	-X--	-----	-----	-----
Microveliidae	-----	---X	-	---X-	-X--	-----	-----	-----	-----
Rhagoveliidae	---X-	-----	-	---X-	-----	-----	-----	-X--	-----
THYSANOPTERA									
Thripidae	-----	XXXX-	-	-----	-----	-----	-----	-----	-----
HOMOPTERA									
Undetermined taxa	-----	---X-	-	---XX	-XXXX	-----	-----	-----	-----
Aphididae	-----	XXXXX	-	-X---	--XX-	-----	-----	-----	-----
Cercopidae	-----	-----	-	---X-	--XX	-----	-----	-----	-----
TRICHOPTERA									
Undetermined adults	-----	--X-X	-	-----	--XXX	--X-X	--X-	-----	XX---
Helicopsychidae larvae	--X--	-----	-	-----	-----	-----	-----	-----	-----
Hydropsychidae larvae	X-XXX	-XXXX	+	-XXXX	--XXX	-XXXX	--XXX	XXXXX	----X
Glossosomatidae larvae	--XXX	--XXX	-	--XX-	--XX-	--XX-	-X--	-XXXX	--X--
Hydroptilidae larvae	X-X-X	-X---	+	-----	-----	-----	-----	-XXX-	-----
Limnophilidae larvae	-X--	-----	-	-----	-----	-----	-----	-----	-----
DIPTERA									
Chironomidae adults	-----	XXXXX	-	XXXXX	X-XXX	---X-	-----	X--X-	X----
Chironomidae larvae and pupae	XXXXX	XXXXX	+	XXXXX	-XXXX	XXXXX	XXXXX	XXXXX	XXXXX
Simuliidae adults	-----	XX-XX	-	--X-	-X-X-	-----	-----	-----	-----
Simuliidae larvae and pupae	XXXXX	XXXXX	+	XXX-X	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX
Tabanidae larvae	--X--	-----	-	-X--	-----	-----	--X-	--XX	-----
Ceratopogonidae larvae	XXX--	XXXX-	-	X----	X-X-	-XX--	-----	X-X-X	-----
Tipulidae adults	-----	-----	-	-----	-----	--X-	-----	-----	-----
Tipulidae larvae	-----	X----	-	X----	X-X-	-----	-----	--X-	-----
Dixidae larvae	---X	XX-X-	-	XX---	-X-	-X---	-----	-----	-----
Ephyridae larvae	X----	X--X	-	X----	X--XX	-----	-----	X--XX	-----
Muscidae larvae	---X-	-----	-	X----	-----	-----	-----	-----	-----
Stratiomyiidae larvae	-----	--X-X	-	-X--	-----	-X--	-----	--XX	-----
Empididae larvae	---X	X----	-	-----	-----	-----	X--X	-----	-----
Culicidae larvae	-----	X-X-	-	---X	-X--	-----	-----	---X-	-----

¹Na. = not applicable.

Table 1 continued.

Items	Benthos	Drift	<i>Gila</i>	<i>Agosia</i>	<i>Meda</i>	<i>Rhin- ichthys</i>	<i>Tiaroga</i>	<i>Catos- tomus</i>	<i>Pant- osteus</i>
LEPIDOPTERA									
Undetermined terrestrial adult	----	----	-	----	----	----	----	--X-	----
Pyralidae larvae	-X--	-X-X-		----	--X-	----	----	--X-	----
MEGALOPTERA									
Corydalidae larvae	----X	----	-	----	--X-	----	----	--X-	----
COLEOPTERA									
Undetermined terrestrial adults	----	XXXX-	-	--XX-	--XX-	----X	----	----	----
Curculionidae adults	----	----	-	----	----	----	----	--X-	----
Hydrophilidae adults	----	X-X--	+	----	----	----	----	----	----
Elmidae larvae	----X	X-XX-	-	----	----	----	----	--X-X	----
Dytiscidae larvae	----	X--X-	+	X--X	----	----	----	XX--	----
Staphylinidae adults	----	--XX-	-	----	--X-	----	----	----	----
Halipidae larvae	----	XX--	+	--X-	----	----	----	----	----
Dryopidae adults	----	----	+	----	----	----	----	----	----
HYMENOPTERA									
Undetermined terrestrial taxa	----	----	-	----	--X-	----	----	----	----
Ichneumonidae	----	----	+	----	----	----	----	----	----
Chalcidoidea	----	XXXX-	-	----	----	----	----	----	----
Formicidae	----	X-X--	+	----	--X-	----	----	----	----
MALLOPHAGA									
Undetermined terrestrial taxa	----	-XXX-	-	-X--	----	----	----	----	----
ACARINA									
Undetermined taxa	XXXXX	XXXXX	-	----	----	--X-	----	X-XXX	-X--
ARANEIDA									
Undetermined taxa	----	--X--	-	----	----	----	----	---X	----
CRUSTACEA									
Ostracoda (Cypridae)	--XXX	XXXXX	-	XXX-X	----	--X-	----	XXX-X	X----
Cladocera (Chydoridae)	----	-XX-X	-	----	----	----	----	---X	----
Copepoda (Cyclopoidea)	----	XXXXX	-	----	----	----	----	-X--	----
TARDIGRADA									
Undetermined terrestrial taxa	----	-X--	-	----	----	----	----	----	----
ANNELIDA									
Undetermined Oligochaeta	XX-XX	XXXXX	-	--X--	-X--	----	XX--	--X--	--X--
Undetermined Hirudinea	--X--	----	-	----	----	----	----	----	----
NEMATODA									
Undetermined taxa	X--X	XX--	-	XX--	--XX-	--X-	----	XXX-X	-XXXX
TURBELLARIA									
Planariidae	--X--	----	-	----	----	----	----	XXXXX	--X-X
HYDRAZOA									
Hydridae	---X	XXX-X	-	----	----	----	----	----	----
VERTEBRATA									
<i>Meda fulgida</i>	----	----	+	----	----	----	----	----	----
<i>Agosia chrysogaster</i>	----	----	+	----	----	----	----	----	----
<i>Sceloporus magister</i>	----	----	+	----	----	----	----	----	----
PLANT MATERIALS									
Diatoms	XXXXX	XXXXX	-	-XXXX	----	----	----	----	XXXXX
Filamentous algae	XXXXX	XXXXX	+	XXXXX	X----	X-X-	----	---X	--XXX
Detritus	XXXXX	XXXXX	+	XXXXX	--XX	--XX-	----	X--XX	---X-
INORGANIC MATERIALS									
Sand	Na. ¹	Na.	+	-XXX-	----	--XX-	----	---X	XXXXX

opened in the laboratory. The ingested animals were sorted to taxonomic categories in a gridded Petri dish. Other categories were inorganic materials (principally sand), finely divided organic material (detritus), filamentous algae, and diatoms. The volume of stomach occupied by each item was estimated visually using Hynes' (1950) point system. Each item in a stomach was assigned a value from greater than 0.0 to a maximum of 20.0, with the last indicating that 100 percent was represented by that item, and that the stomach was full. Each point, therefore, was equivalent to 5.0 percent of the total estimated stomach volume. Empty stomachs were scored 0.0 points and are included in compilations. Relative strengths and weaknesses of this technique were detailed by Hynes (1950) and Corbet (1961), who found estimation of relative volumes did not differ significantly from methods where quantities were measured directly. Actual volume of items or parts of items present were assigned points. No attempt was made to reconstruct live volumes of invertebrates from fragments (Ricker 1937).

Data for standing crops of benthic invertebrates were provided by Dale A. Bruns, ASU (Bruns 1977, Bruns and Minckley 1980). The drifting component of potential and actual food for fishes was collected by drift net and techniques described by Waters (1962). Sampling and analytic techniques, and tabular quantitative data on benthos and drift, are presented by Schreiber (1978) and are discussed here only in general terms relative to feeding of fishes.

Marked diel periodicity of drift of aquatic invertebrates (Waters 1962, 1972), and of feeding of fishes (Ivlev 1961), were compensated for by computing means for each over the 28-hour sampling periods. Standing crops of benthos were estimated by the mean of two samples per period. Compilation of data was performed on a Univac 1110/42 computing system (Arizona State University Computing Center).

RESULTS

Foods Available to Fishes

A total of 75 potential or actual food items was taken in samples of benthos, drift, and fish stomachs from Aravaipa Creek (Table 1). Of these, 69 (93.3 percent) were invertebrates. Vertebrates (three species) were eaten only by roundtail chub, and species diversity of plant materials was not assessed. Inorganic material (sand) was excluded from the gross number of items, but was common in stomachs of *Pantosteus clarki* and occasionally in *Agosia chrysogaster*, *Rhinichthys osculus*, and *Catostomus insignis*.

Of invertebrate taxa, 36 kinds (52.2 percent) were nymphs, pupae, or nonemerging adults of aquatic insects. Noninsect aquatic animals made up 13 percent (9 groups), emergent adults of aquatic groups, 8.8 percent (6 groups), and 26.1 percent (18 taxa) were of terrestrial origin.

Only a few invertebrate taxa were consistently present in both benthos and drift samples (Table 1). Genera of the family Baetidae (*Baetis*, *Callibaetis*, and *Centroptilium*) comprised most of the mayfly biomass, and they were also highest in numbers. Tricorythidae (*Tricorythodes*) and Leptophlebiidae (*Choroterpes* and *Leptohypes*) were far less abundant than Baetidae, but were equally as frequent in occurrence. Heptageniidae (*Rithrogena*) and Ephemerellidae (*Ephemerella*) nymphs were seasonally abundant (winter-spring) in benthic samples and were present in drift during the same periods.

Larvae and pupae of the dipteran families Chironomidae and Simuliidae were present in all periods, both in drift and benthic samples. They were relatively important in terms of biomass, and were often present in large numbers. Adult chironomids were present in all drift samples, forming significant proportions of the biomass. Adult simuliids were uncommon in drift, but were taken in 4 of 5 sampling periods.

Water mites (Acarina) and microcrustaceans, especially cyprid ostracods, also were relatively consistent in occurrence in benthic and drift samples, but were of minor consequence in biomass.

Trichopteran larvae of the genera *Hydropsyche* and *Cheumatopsyche* (Hydropsychidae) were scarce early in the study, but became important later as major components of biomass in benthic samples and as relatively common taxa in drift. Glossosomatidae trichopterans followed a similar trend. High biomass estimates for trichopterans, especially Hydropsychidae, typically resulted from a few large individuals rather than from dense populations.

A large number of other animals were in benthic and drift samples (Table 1), some in small numbers or only occasionally, and others seasonally. Especially seasonal in abundance was the Capniidae plecopteran, *Mesocapnia frisoni*, occurring only during cool weather, and turbellarians in the benthos in summer.

Interrelations of Benthos and Drift

Variance in samples from benthic communities is notoriously high (Elliott 1971), presumably as a result of heterogeneity of stream habitats joined with diversified life histories and behaviors of faunal constituents. Drift of certain organisms (*i.e.*, Baetidae) has, however, been demonstrated as consistent and predictable, and has been proposed as a measure of invertebrate populations in streams that may be more sensitive than direct sampling of benthos (Waters 1965, 1972). Mixing action of turbulence tends to suppress effects of heterogeneity.

The relationship between drift and standing crop of benthos at a given place is only a general one, especially if habitats upstream vary significantly from that at the point of sampling. Waters (1965) estimated on the basis of blocking a stream that organisms drifting at a given place originated no more than 50 or 60 m upstream. Our comparisons of standing crops of benthos and drift were justified by similarity of habitat throughout the reach and by lack of statistical differences in numbers and biomass at our station and another site immediately above (Bruns 1977). Samples of drift and benthos were always taken midway in a 60-m-long, uniform riffle, so comparative integrity of data was maintained.

A total of 36 items occurred in samples of benthos: 26 (72.2 percent) were nymphs, larvae, pupae, and nonemerging adults of aquatic insects, 7 (19.4 percent) were other aquatic invertebrates, and 3 (8.3 percent) were non-animal categories (algae, diatoms, and detritus). Drift sampling caught items of 66 taxa. Of these, 27 (49.1 percent) were aquatic insects, 5 (9.1 percent) were emergent adults of aquatic insects, 7 (12.7 percent) were other aquatic invertebrates, and 13 (23.6 percent) were invertebrates of terrestrial origin. Three (5.5 percent) were the nonanimal components defined above.

Invertebrates common to drift and benthos included all important categories discussed before (Table 1). Slightly more than 65 percent of drift (excluding nonanimal components) was derived from benthos, and this rose to 75 percent when emerged adults of aquatic insects were included. Three of four items in drift of Aravaipa Creek were, therefore, autochthonous to the system. Of 32 benthic taxa recorded (again excluding nonanimal items), 23 (71.4 percent) drifted. Groups of benthic animals absent from drift included Libellulidae (dragonflies), Tabanidae (horseflies), Muscidae (muscid flies), Rhagoveliidae (water striders), Helicopsychidae and Limniphilidae (caddisflies), Corydalidae (hellgrammites), Hirudinae (leeches), and Turbellaria (flatworms). Absence of all but the last from drift may be generally attributed to their rarity. Turbellarians appeared to resist drifting. Of organisms drifting, only baetids and *Tricorythodes* mayflies and chironomid dipteran larvae and pupae were present in all samples on all sampling dates.

Foods of Fishes

Nymphal mayflies comprised 57 percent or more of stomach contents of 5 of 6 fish species analyzed quantitatively (Fig. 2). Only the herbivorous *Pantosteus clarki* contained few ephemeropterans. Dipteran larvae were most common in stomachs of bottom-dwelling fishes, *Rhinichthys osculus*, *Tiaroga cobitis*, and *Catostomus insignis*. Trichopteran larvae were less than 10 percent of total food volumes in all but *T. cobitis*, but present in significant amounts in all but *P. clarki* stomachs.

Plecopteran nymphs were also eaten in small amounts by all species, but *P. clarki* contained only traces of that taxon (Fig. 2). Turbellaria were heavily preyed upon by *C. insignis* and *P. clarki* when present in summer, but not by other fishes. Winged insects (including both emerged aquatic forms and scarcer terrestrial kinds) were consumed in more than trace amounts by *Meda fulgida*, *Agosia chrysogaster*, and *R. osculus* in decreasing order of volumes. Other than *P. clarki*, only *A. chrysogaster* consumed substantial amounts of vegetative material. Animals eaten in volumes too low for visual quantification in Figure 2 are listed in Table 1. When all potential foods are considered, 66 (88 percent) of the 75 items were found in at least one species of fish.

Accounts of Species

ROUNDTAIL CHUB.— Chubs (*Gila robusta*) ate 21 items, including many principal foods of other species (Table 1). The diet strongly reflected its large body size (to 38.5 cm total length in Aravaipa Creek), expansive, terminal mouth, and raptorial pharyngeal teeth. Many food items were large in size, and mastication was apparent (Burton, pers. comm.). Chubs are secretive animals, inhabiting deeper water near cover; yet occurrence of terres-

trial organisms such as an iguanid lizard and ants, and a variety of benthic inhabitants (e.g., Odonata naiads), other fishes, and Belostomatidae hemipterans, indicates active feeding from bottom to surface. Uniqueness of this diet was exemplified by only 38.1 percent of the food items also being consumed by other fish species. Six (28.6 percent) items found in *Gila robusta* stomachs did not appear in other fishes.

LONGFIN DACE.— Thirty-nine kinds of foods were tallied from stomachs of *Agosia chrysogaster*, and algae made up a substantial proportion of the diet (Table 2, Fig. 3). *Cladophora glomerata*, the dominant filamentous alga in the channel (Bruns and Minckley 1980), was rarely present. Diatoms and unattached green algae (*Mougeotia* sp. and *Spirogyra* sp.) were abundant in stomachs, and blue-green filamentous forms such as *Oscillatoria* sp. occasionally were present. These organisms are characteristic of stream margins and quiet areas near beds of higher plants, and their presence reflected grazing by longfin dace in such places.

Fisher et al. (1981) considered longfin dace to be herbivorous in Sycamore Creek, Arizona, but large volumes of invertebrates were in stomachs from Aravaipa Creek. Of ephemeropteran nymphs eaten by longfin dace, the ubiquitous baetids predominated in 4 of 5

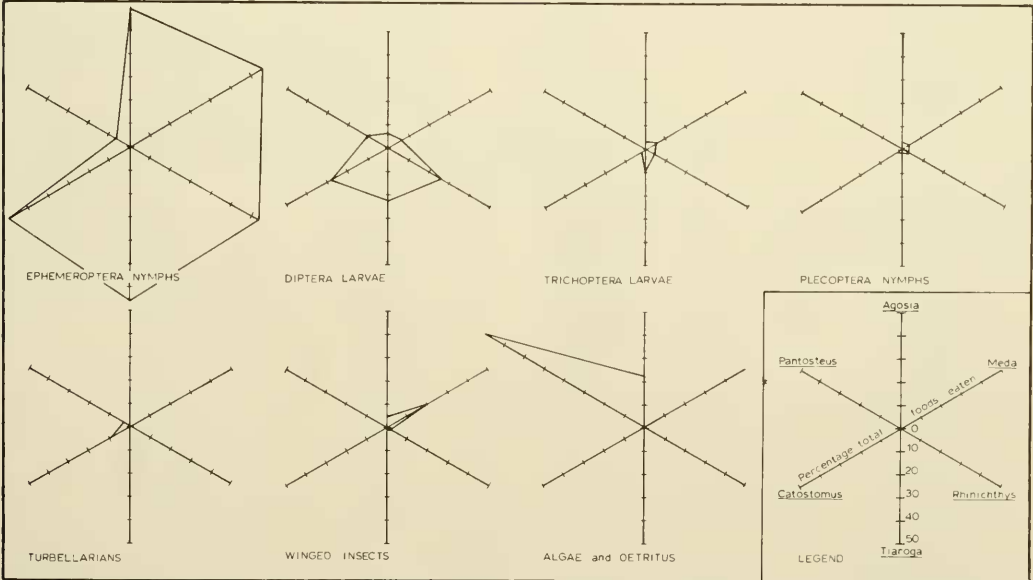


Fig. 2. Annual averages of relative percentages of major food items eaten by six species of fishes in Aravaipa Creek, Arizona, 1975-1976.

sampling periods (ranging from 23 to 61.4 percent of total foods). Relationship between drift biomass of baetids and occurrence in longfin dace stomachs seemed strong ($r = 0.81$). There was no obvious relationship between benthic standing crop and stomach contents ($r = <0.5$). *Tricorythodes* mayflies were preyed upon in all but the January 1975 period, occupied more volume in April than did baetids (36.5 percent vs. 24.2 percent), and were eaten in substantially smaller amounts than baetids in the periods July 1975 through January 1976. *Tricorythodes* spp. rarely achieved half the numbers or biomass of baetids in drift or benthos (Schreiber 1978); thus some special association with longfin dace was indicated. The three species recorded by Bruns (1977) from Aravaipa Creek, *T. condylus*, *T. dimorphus*, and *T. minutus*, were most abundant in sand-bottomed areas. Longfin dace shared this tendency to be most abundant in open, sandy areas, with moderate current, in water <10 cm deep (especially in periods of lower light intensity; Minckley and Barber 1971).

Leptophlebiidae and *Rhithrogena* sp. mayflies made up only a small proportion of the diet of longfin dace. The former were present as 14 percent of total food volume in July and were absent or in trace amounts in other months (Table 3), despite their consistent presence in both benthos and drift (Table 1).

The common leptophlebiids (*Choroterpes inornatus*) and *Rithrogena* sp. are both rheophilic and associated with cobble-bottomed rapids in Aravaipa Creek (Bruns 1977), a habitat rarely occupied by longfin dace. *Rhithrogena* sp. was, however, present in stomachs of *A. chrysogaster* in their period of occurrence (January of both years).

Plecopteran nymphs were eaten during their winter occurrence. Appearance of Hydropsychidae larvae (Trichoptera) in stomachs corresponded well with a spectacular increase in their biomass in benthos in January 1976—and with an increase in drift during that period, although far less impressive (Schreiber 1978). The increase in volumes eaten resulted from a few large individuals, rather than from increases in numbers, as also occurred in benthos samples.

Dipteran larvae made up a substantial percentage of total food in *A. chrysogaster* only in January 1975, the same period during which chironomid and simuliid larvae were most common in drift. A gradual decline in drift of dipterans throughout the study was paralleled by a continuing drop in volumes in the diet. Occurrences of Chironomidae and Simuliidae in benthic samples were consistent, but variations in standing crops did not correspond to those in stomachs. Chironomids are a diverse group, generally distributed within the stream. The small

TABLE 2. Food habits of longfin dace, *Agosia chrysogaster*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parenthesis.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (70)	Apr (32)	Jul (40)	Oct (40)	Jan (41)	Jan	Apr	Jul	Oct	Jan
EPEHEMEROPTERA NYMPHS	9.7	17.8	4.7	6.2	24.9	45.1	60.7	47.0	68.9	66.8
Baetidae	8.6	7.1	2.3	3.9	22.9	40.0	24.2	23.0	43.3	61.4
Tricorythidae	—	10.7	1.0	2.3	2.0	—	36.5	10.0	25.6	5.4
Leptophlebiidae	Tr.	—	1.4	Tr.	—	Tr.	—	14.0	Tr.	—
Heptageniidae	1.1	—	—	—	Tr.	5.1	—	—	—	Tr.
PLECOPTERA NYMPHS (Capniidae)	2.2	—	—	—	1.1	10.2	—	—	—	3.0
TRICHOPTERA LARVAE (Hydropsychidae)	—	Tr.	Tr.	Tr.	3.5	—	Tr.	Tr.	Tr.	9.4
DIPTERA LARVAE, PUPAE	6.1	1.3	Tr.	Tr.	Tr.	28.4	4.4	Tr.	Tr.	Tr.
Chironomidae	3.7	Tr.	Tr.	Tr.	Tr.	17.3	Tr.	Tr.	Tr.	Tr.
Simuliidae	2.4	1.3	Tr.	Tr.	Tr.	11.2	4.4	Tr.	Tr.	Tr.
WINGED INSECTS	1.4	3.7	Tr.	Tr.	6.5	12.6	Tr.	Tr.	Tr.	Tr.
Ephemeroptera	—	3.7	—	Tr.	Tr.	6.5	12.6	Tr.	Tr.	Tr.
Chironomidae	1.4	Tr.	Tr.	Tr.	Tr.	6.5	Tr.	Tr.	Tr.	Tr.
ALGAE (Filamentous algae)	2.1	6.5	5.3	2.8	7.8	9.8	22.2	53.0	31.1	20.8

occurrence of rheophilic simuliids, however, tends to substantiate a lack of feeding by longfin dace on turbulent riffles.

Winged insects in stomachs of longfin dace, especially trace amounts of terrestrial coleopterans and homopterans (Table 1), indicated some feeding at the surface. Nevertheless, correspondence of frequencies of adult ephemeropterans and chironomids in drift and in stomachs was far less than perfect. Both taxa drifted throughout the year,

and chironomids were consistently taken by *A. chrysogaster* and mayflies were not. Perhaps the relatively larger size of some adult mayflies caused the small-mouthed longfin dace to select against them. The dace ate more mayfly adults in April, although they drifted most abundantly in January of both years, and more chironomid adults were eaten in January 1975 than in January 1976, when they were equally abundant in drift.

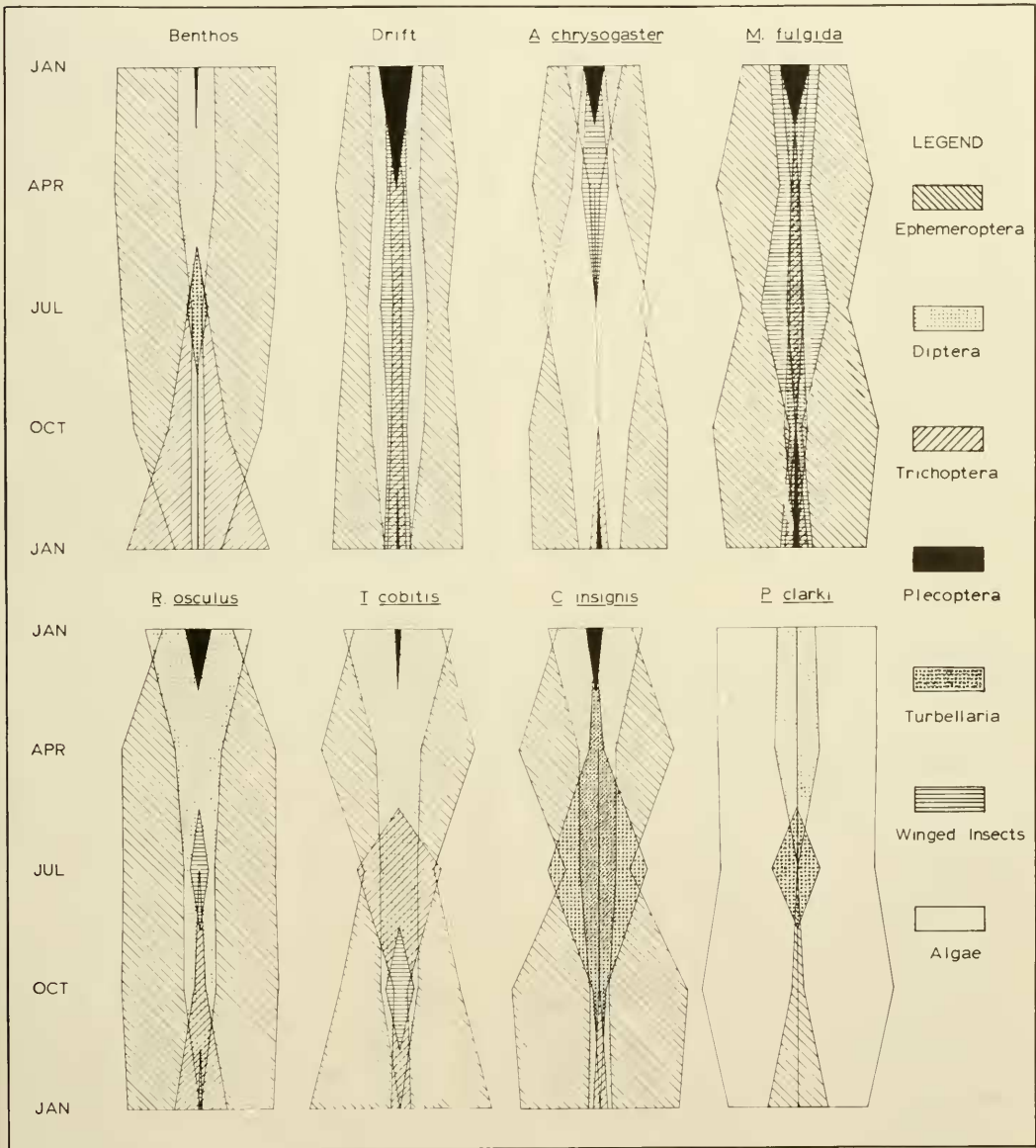


Fig. 3. Relative abundance (by weight) of major invertebrate taxa in benthos and drift, and of invertebrate taxa and algae in stomachs (by volume) of fishes from Aravaipa Creek, Arizona, 1975-1976.

SPIKEDACE.— Patterns of use of nymphal ephemeropterans by *Meda fulgida* in Aravaipa Creek closely followed those just described for *Agosia chrysogaster* (Table 3). Spikedace occupy pools, or areas of deeper water below riffles (Miller and Hubbs 1960). In Aravaipa Creek, where pools are essentially absent, it is typically found in middle to surface depths of deeper parts of the channel, or in riffles and runs of moderately swift current. Spikedace are relatively small (<75 mm total length), highly mobile fish, moving continuously and visually inspecting drifting materials at the surface and within the water column. Gustatory inspection also is commonly practiced, items being taken into the large, terminal mouth, moved about, then swallowed or rejected. The 36 food items recovered from stomachs illustrates its versatility. A high percentage (22 percent) of terrestrial organisms, few of which were eaten by other species (Table 1), produced a diet qualitatively as unique as that of *Gila robusta*.

Total volumes of Baetidae in stomachs and biomass of drift did not correlate as highly for *M. fulgida* ($r = 0.68$) as it did for *A. chrysogaster*. Baetids in benthos were not related to total volumes in spikedace stomachs ($r = <0.5$). *Tricorythodes* spp. nymphs in benthos were correlated with total volumes

in spikedace ($r = 0.91$), but no such relationship was apparent between stomach volumes and drift ($r = <0.5$). Again, sandy bottomed areas of the channel occupied by both *Tricorythodes* spp. nymphs and spikedace presumably enhanced their interrelationship. Leptophlebiids, *Rhithrogena* sp., and *Ephemerella* sp. nymphs made up only minor parts of the diet. The first of these did, however, contribute 13 percent in a single sampling period (July).

Plecoptera nymphs were used by spikedace when present, most frequently in January 1978, when they were also most common in drift (Fig. 3). Hydropsychid larvae (Trichoptera) were in stomachs in all but the first sampling period and were major contributors to total food volume in July 1975 and January 1976. These organisms made up a disproportionate percentage in July (8 percent) as compared to their low relative abundance in benthos and drift (2.7 and 1.5 percent, respectively), perhaps indicating selection by the fish.

Spikedace fed more heavily upon winged insects than did any other fish species in Aravaipa Creek, with an average total volume throughout the study of more than 20 percent (Figs. 2–3). Mayfly adults were generally most abundant, paralleled or closely followed by chironomid adults. Opportunism seemed

TABLE 3. Food habits of spikedace, *Meda fulgida*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (28)	Apr (22)	Jul (33)	Oct (37)	Jan (20)	Jan	Apr	Jul	Oct	Jan
EPHEMEROPTERA NYMPHS	28.2	50.7	19.2	20.4	41.8	52.2	78.0	53.0	83.0	69.6
Baetidae	24.4	36.6	9.6	17.7	40.5	45.3	56.3	26.5	72.0	67.5
Tricorythidae	2.0	12.4	4.9	2.7	1.3	3.6	19.1	13.5	11.0	2.1
Heptageniidae	1.8	—	—	—	—	3.3	—	—	—	—
Leptophlebiidae	Tr.	Tr.	4.7	Tr.	—	Tr.	Tr.	13.0	Tr.	—
Ephemerellidae	—	1.7	—	—	—	—	2.6	—	—	—
PLECOPTERA NYMPHS (Capniidae)	7.0	—	—	Tr.	1.5	12.9	—	—	Tr.	2.5
TRICHOPTERA LARVAE (Hydropsychidae)	—	1.7	2.9	Tr.	7.3	—	2.6	8.0	Tr.	12.1
DIPTERA LARVAE, PUPAE	7.4	2.8	2.0	2.8	Tr.	13.8	4.4	5.5	11.5	Tr.
Chironomidae	5.0	1.4	2.0	Tr.	Tr.	9.3	2.2	5.5	Tr.	Tr.
Simuliidae	2.4	1.4	Tr.	2.8	Tr.	4.5	2.2	Tr.	11.5	Tr.
WINGED INSECTS	11.2	9.8	12.1	1.4	9.5	20.5	15.1	33.5	5.5	15.8
Ephemeroptera	7.0	9.8	Tr.	1.4	6.0	12.9	15.1	Tr.	5.5	10.0
Chironomidae	4.2	Tr.	1.5	Tr.	Tr.	7.6	Tr.	4.2	Tr.	Tr.
Trichoptera	—	—	10.6	Tr.	3.5	—	—	29.3	Tr.	5.8

the rule in *M. fulgida*, and active feeding on emerging trichopterans was apparent in July. Trichopteran adults made up 29.3 percent of total volume of the diet in that sampling period (Table 3).

SPECKLED DACE.— This dace has a strong proclivity for riffles within a broader range of habitat selection (Minckley 1973). Its diet in Aravaipa Creek, which consisted largely of rheophilic insects (Table 4), reflected this habitat preference. Food habits of *Rhinichthys osculus* overlapped widely with those of *Agosia chrysogaster* and *Meda fulgida*, however, with more than 80 percent of its foods also eaten by the other two fishes.

Ephemeropteran nymphs made up more than 70 percent of total food volume in *R. osculus* in all but the first sampling period (Figs. 2–3). *Tricorythodes* and leptophlebiid nymphs, species of sand-bottomed channels and cobble-bottomed rapids, respectively, had a combined volume exceeding that of baetids in April and July (Table 4). This resembled the pattern for *A. chrysogaster* in the same periods (Table 2), but was distinct from that for *M. fulgida* (Table 3), where baetids dominated stomach contents.

Plecopteran nymphs were preyed upon when present in winter, and in greatest quantities in January 1975. Hydropsychid larvae (Trichoptera) increased in importance from July 1975 to become a major component of

total foods consumed in January 1976, following the increase in caddisflies in both benthos and drift.

Dipteran larvae and pupae were more heavily used by the bottom-feeding speckled dace than by either longfin dace or spike-dace. High initial levels of predation by *R. osculus* on dipterans gradually declined, however, parallel to indicated availability; simuliids were heavily used, further documenting foraging by speckled dace in riffles.

Trichopteran adults were taken by *R. osculus* in July and January 1976. Because speckled dace rarely move near the surface, it is likely adult caddisflies were caught during emergence from benthic puparia. Only one of 23 food items recorded for speckled dace was of terrestrial origin (Table 1), further supporting the rarity of surface feeding by this minnow.

LOACH MINNOW.— This species was rare in Aravaipa Creek during the period. A total of 47 individuals was examined, with a range per sampling period of 3 to 14 individuals (Table 5). This diminutive minnow is current loving and benthic in habit, living exclusively on riffles <15 cm deep (Minckley 1965, 1973).

This restriction in habitat was manifested in an equally limited diet (Figs. 2–3). Only 11 items were tallied from stomachs of *Tiaroga cobitis*, and only 2 are sometimes associated

TABLE 4. Food habits of speckled dace, *Rhinichthys osculus*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parenthesis.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (12)	Apr (6)	Jul (38)	Oct (36)	Jan (34)	Jan	Apr	Jul	Oct	Jan
Ephemeroptera nymphs	17.1	27.5	23.3	17.7	16.8	34.7	76.8	76.2	79.0	72.9
Baetidae	15.0	8.3	10.3	16.5	16.8	30.5	23.3	33.6	73.3	71.1
Tricorythidae	—	10.0	5.8	1.2	Tr.	—	27.9	18.9	5.3	1.8
Heptageniidae	2.1	—	—	—	Tr.	4.2	—	—	—	Tr.
Leptophlebiidae	—	6.7	7.2	—	—	—	18.6	23.7	—	—
Ephemerellidae	—	2.5	—	—	—	—	7.0	—	—	—
Plecoptera nymphs (Capniidae)	6.3	—	—	—	Tr.	12.7	—	—	—	Tr.
Trichoptera larvae (Hydropsychidae)	—	—	Tr.	1.0	6.2	—	—	Tr.	4.6	26.1
Diptera larvae, pupae	25.8	8.3	4.7	3.7	Tr.	52.6	23.3	15.0	16.3	Tr.
Chironomidae	5.8	5.8	1.9	1.8	Tr.	11.9	16.3	7.0	7.9	Tr.
Simuliidae	20.0	2.5	2.8	1.9	Tr.	40.7	7.0	9.0	8.5	Tr.
Winged insects (Trichoptera)	—	—	2.6	—	Tr.	—	—	8.6	—	1.1

with nonriffle habitats (*Tricorythodes* spp. nymphs and Tabanidae dipteran larvae, the latter occurring only as a trace; Table 1). Ubiquity of baetid nymphs and chironomid larvae reduce their value in interpretation of feeding habitats of the minnow, but both are common on riffles. Cobble-inhabiting, swift-water forms such as *Rhithrogena* sp. and leptophlebiid nymphs reflect occupation of riffles by the fish, as do the large percentage of simuliids eaten early in the study (Table 5). Of other fishes in the stream, only *Gila robusta* used less than 80 percent of the same food items depended upon by *T. cobitis*, and most species ate more than 90 percent.

Ephemeropteran nymphs made up most of the diet of *T. cobitis* during three sampling periods. Baetids were most important in each instance. *Tricorythodes* spp. nymphs were abundant in stomachs only in April, leptophlebiids were similarly abundant in July 1975 and January 1976, and *Ephemerella* sp. were eaten in moderate quantities when abundant in April (Table 5). Active selection for trichopteran larvae by loach minnows was indicated in July. Neither family of caddisfly larvae that were consumed were abundant in drift or benthos at that time; yet hydropsychids made up 28.2 percent of total food volume, and glossosomatids 18.8 percent. Neither group was in stomachs in January and April 1975 (perhaps because of small sample size in April), and only hydropsychids persisted in October 1975 and January 1976.

The gradual decline in percentages of dipteran larvae in stomachs of other minnow species throughout the study was less pronounced in *T. cobitis* because of its cropping of simuliids in all but the last sampling period. Chironomid larvae were a minor component of diet of the loach minnow (Table 5).

Winged trichopterans appeared in stomachs in October, presumably being captured upon emergence from puparia. Loach minnows cannot maintain position in midwater without violent swimming, due in part to a greatly reduced air bladder. Feeding from the surface or even midwater in areas of turbulence is therefore unlikely. It is interesting, however, that regression coefficients between stomach volumes of *T. cobitis* and some components of drift were relatively high (e.g., for total ephemeropterans, $r = 0.86$), and no such relationships were apparent between benthic biomass and stomach contents. The fish may directly sample areas from which drift is derived, and the gross estimation of benthic communities afforded by our sampling was far less adequate.

SONORA SUCKER.— This large species exhibited a generalized, carnivorous diet in Aravaipa Creek. The fish is typically a pool dweller (Minckley 1973), living on the bottom in areas near undercut banks, boulders, or logs and other debris. It will sometimes visit midwater and, despite the ventral mouth, has been observed taking foods there. Although the diet of *Catostomus insignis* was

TABLE 5. Food habits of loach minnow, *Tiaroga cobitis*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (12)	Apr (3)	Jul (14)	Oct (12)	Jan (6)	Jan	Apr	Jul	Oct	Jan
EPHEMEROPTERA NYMPHS	30.0	35.0	9.8	16.5	55.8	43.7	77.7	34.6	61.6	90.6
Baetidae	30.0	25.0	7.5	16.5	47.5	43.7	55.6	26.5	61.6	77.1
Tricorythidae	—	7.5	Tr.	Tr.	2.5	—	16.7	Tr.	Tr.	4.1
Leptophlebiidae	Tr.	—	2.3	Tr.	5.8	Tr.	—	8.1	Tr.	9.4
Ephemerellidae	—	2.5	—	—	—	—	5.5	—	—	—
PLECOPTERA NYMPHS (Capniidae)	1.4	—	—	—	—	2.0	—	—	—	—
TRICHOPTERA LARVAE	—	—	13.3	1.5	5.8	—	—	47.3	5.6	9.4
Hydropsychidae	—	—	8.0	1.5	5.8	—	—	28.2	5.6	9.4
Glossosomatidae	—	—	5.3	—	—	—	—	18.8	—	—
DIPTERAN LARVAE, PUPAE	37.3	10.0	5.2	5.0	Tr.	54.3	22.2	18.3	18.1	Tr.
Chironomidae	6.8	2.5	Tr.	Tr.	Tr.	9.9	5.5	Tr.	Tr.	Tr.
WINGED INSECTS (Trichoptera)	—	—	—	3.8	—	—	—	—	14.3	—

almost as diversified as that of *Agosia chrysogaster* (38 items, Table 1), the average overlap with other fishes in Aravaipa Creek was only 44.3 percent (range 26.3 to 68.4 percent). Most foods unique to the sucker were tiny, bottom-dwelling forms such as Acarina and microcrustaceans (Table 1).

Baetid nymphs were important to *C. insignis* through much of the study, but *Tricorythodes* spp. nymphs became progressively more so and were the dominant mayfly in stomachs in January 1976 (Table 6). Abundance of *Tricorythodes* spp. nymphs in benthos and drift did not follow that same pattern. *Ephemerella* sp. nymphs were abundant in stomachs only in April, and plecopteran nymphs contributed significantly to the diet only in January 1975. The only significant trichopteran larvae were glossosomatids, present in greatest volumes in January 1976 at their peak of density in benthos.

Dipteran larvae made up the largest portion of stomach contents in January 1975 and tended to decrease in relative volume with time (Table 6). Chironomids were consistently important in stomachs of *C. insignis*, fluctuating erratically with respect to indicated availability. Simuliid larvae were significant only in the first two sampling periods.

Summer-active turbellarians were heavily used by Sonora suckers (Figs. 2–3), with some

individual fish containing them exclusively in July, the period of peak abundance of the flatworm in the benthos (Bruns and Minckley 1980).³

Of foods eaten by *C. insignis*, *Ephemerella* sp., simuliids, and glossosomatids are characteristic of swift-water habitats. Their sporadic and low occurrences in stomachs may be explained by drift into pools, where consumed, or by infrequent visits of individual suckers to riffles. Nine of the other 28 invertebrate taxa that occurred in *C. insignis*, but were too rare to quantify (Table 1), also were characteristic of swift areas. Fifteen taxa were typical of stream margins or pool-like habitats, and 4 were winged adults of aquatic insects or were derived from terrestrial sources. Diversity in pool-dwelling forms was impressive, with seven families of dipteran larvae and three groups of microcrustaceans, plus oligochaetes and nematodes.

As with *Tiaroga cobitis*, regression coefficients between some stomach contents of *C. insignis* and drift data were interestingly high, but those with benthos were low. Drifting ephemeropteran nymphs vs. stomach volumes in the same period gave $r = 0.80$, and total dipteran larvae in drift against stomach volumes was $r = 0.92$. The only benthic value to exceed $r = >0.5$ was total mayfly nymphs vs. total mayflies in stomachs ($r = 0.58$).

TABLE 6. Food habits of Sonora sucker, *Catostomus insignis*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (7)	Apr (3)	Jul (17)	Oct (17)	Jan (18)	Jan	Apr	Jul	Oct	Jan
Ephemeroptera nymphs	17.6	21.7	7.8	17.1	18.9	37.4	76.4	33.1	84.7	80.9
Baetidae	16.3	16.7	5.3	12.4	9.2	34.7	58.8	22.5	61.4	39.3
Tricorythidae	1.3	1.7	2.5	4.7	9.7	2.7	6.0	10.6	23.3	41.6
Ephemerellidae	—	3.3	—	—	—	—	11.6	—	—	—
Plecoptera nymphs	3.1	—	—	Tr.	Tr.	6.7	—	—	Tr.	Tr.
(Capniidae)										
Trichoptera larvae	—	Tr.	Tr.	Tr.	1.7	—	Tr.	Tr.	Tr.	7.2
(Glossosomatidae)										
Diptera larvae, pupae	26.3	5.0	4.2	1.8	2.8	56.0	17.6	17.9	8.9	11.9
Chironomidae	21.3	1.7	4.2	1.8	2.8	45.3	6.0	17.9	8.9	11.9
Simuliidae	5.0	3.3	Tr.	Tr.	Tr.	10.7	11.6	Tr.	Tr.	Tr.
Turbellaria	Tr.	1.7	11.6	1.3	Tr.	Tr.	6.0	49.0	6.4	Tr.

³Mbida Mpome, ASU (pers. comm.), has identified a parasitic fluke (Trematoda) from Aravaipa Creek catostomids that may have been confused with turbellarians in an unknown number of fish.

DESERT SUCKER.— This species (*Pantosteus clarki*) is associated with more turbulent waters in Aravaipa Creek, moving into riffles and rapids from protected places near boulders, then returning. Large adults frequent strongly flowing, deeper waters near undercut banks and obstructions, often syntopic with *Catostomus insignis*.

Although dipteran larvae were common components of diet in January and April 1975, as were turbellarians in July 1975 and baetid nymphs in January 1976, filamentous algae and diatoms made up the major portion of total foods of *Pantosteus clarki* throughout the study (Table 7, Figs. 2–3). Animal foods may well have been ingested incidental to plants. The high percentages of some animal groups on specific sampling dates, however, (e.g., turbellarians in July) indicate some degree of facultative use.

The maximum standing crops of algae in Aravaipa Creek were in April 1975 and January 1976, and they were minimal in summer and autumn, largely due to scour by summer spates (Bruns and Minckley 1980). The smallest percentages occupied by filamentous algae in *P. clarki* stomachs also were in the last two periods (Table 7). Although the dominant filamentous alga in the channel was *Cladophora glomerata*, only small quantities were ingested by the fish. Genera of algae fed upon included those eaten by *Agosia chrysogaster* (*Mougeotia* and *Spirogyra*) in trace quantities, and scarce *Rhizoclonium*, plus abundant *Oedogonium* and diatoms. The first three genera generally live along shorelines of the stream and the last two taxa are

in the channel on stones and as an abundant epiphyte of *C. glomerata*.

Diatoms also were adversely affected by spates but recovered more rapidly than did the large, attached algae, and rather consistent densities were maintained, especially in winter (Bruns and Minckley 1980, Minckley 1981). When *C. glomerata* choked the channel, *P. clarki* mouthed fronds of the alga and removed attached materials with lateral head movements and sucking action of the mouth. Stomachs contained great quantities of diatoms and *Oedogonium* at that time, and fragments of *C. glomerata* also were ingested. After scour, the sucker scraped epilithic diatom films from stones (in October, Table 7) with the cartilagenous sheaths that cover its upper and lower jaws. Fisher et al. (1981) reported similar foods for desert suckers in Sycamore Creek, Arizona.

DISCUSSION

Fishes in Aravaipa Creek present three obvious trophic patterns. The desert sucker was the only herbivore, the longfin dace was at least a facultative omnivore, and the remaining five fishes were carnivorous. A single order of insects, ephemeropterans, bore the brunt of predation by most fish species (Fig. 3).

Mayfly nymphs averaged more than 60 percent of total diets by volume in four carnivorous fishes for which quantitative data were compiled and also were eaten by the roundtail chub (Table 1) and longfin dace (Table 2). Baetid mayflies were cropped

TABLE 7. Food habits of desert sucker, *Pantosteus clarki*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (41)	Apr (22)	Jul (19)	Oct (21)	Jan (22)	Jan	Apr	Jul	Oct	Jan
EPHEMEROPTERA NYMPHS (Baetidae)	Tr.	Tr.	Tr.	Tr.	4.8	Tr.	Tr.	Tr.	Tr.	29.1
DIPTERA LARVAE, PUPAE	4.9	2.1	Tr.	Tr.	Tr.	19.2	21.5	Tr.	Tr.	Tr.
Chironomidae	3.8	2.1	Tr.	Tr.	Tr.	14.9	21.5	Tr.	Tr.	Tr.
Simuliidae	1.1	Tr.	Tr.	Tr.	Tr.	4.3	Tr.	Tr.	Tr.	Tr.
TURBELLARIA	—	—	1.8	—	—	—	—	22.5	—	—
ALGAE	20.6	7.6	6.2	3.8	11.6	80.8	78.5	77.6	95.6	70.9
Filamentous algae	9.3	4.6	2.9	Tr.	9.1	36.5	47.6	36.3	5.9	55.6
Diatoms	11.3	3.0	3.3	3.8	2.5	44.3	30.9	41.3	89.7	15.3

more extensively than any other group (Tables 2-7), were the most ubiquitous, and had greater biomass than other invertebrates. Occurrences of other families of mayflies in stomachs appeared to reflect differing habitat preferences of predators and prey, and seasonality of life-history phenomena of the latter. On a relative basis, mayfly nymphs remained remarkably uniform in benthic

biomass throughout the study, being reduced in relative importance by increases in hydropsychid trichopterans only in the last two sampling periods (Fig. 3). Relative importance of mayfly nymphs by weight remained uniform in drift samples. Absolute values for benthos and drift, however, varied substantially from period to period (Fig. 4). Total drift was lowest after sum-

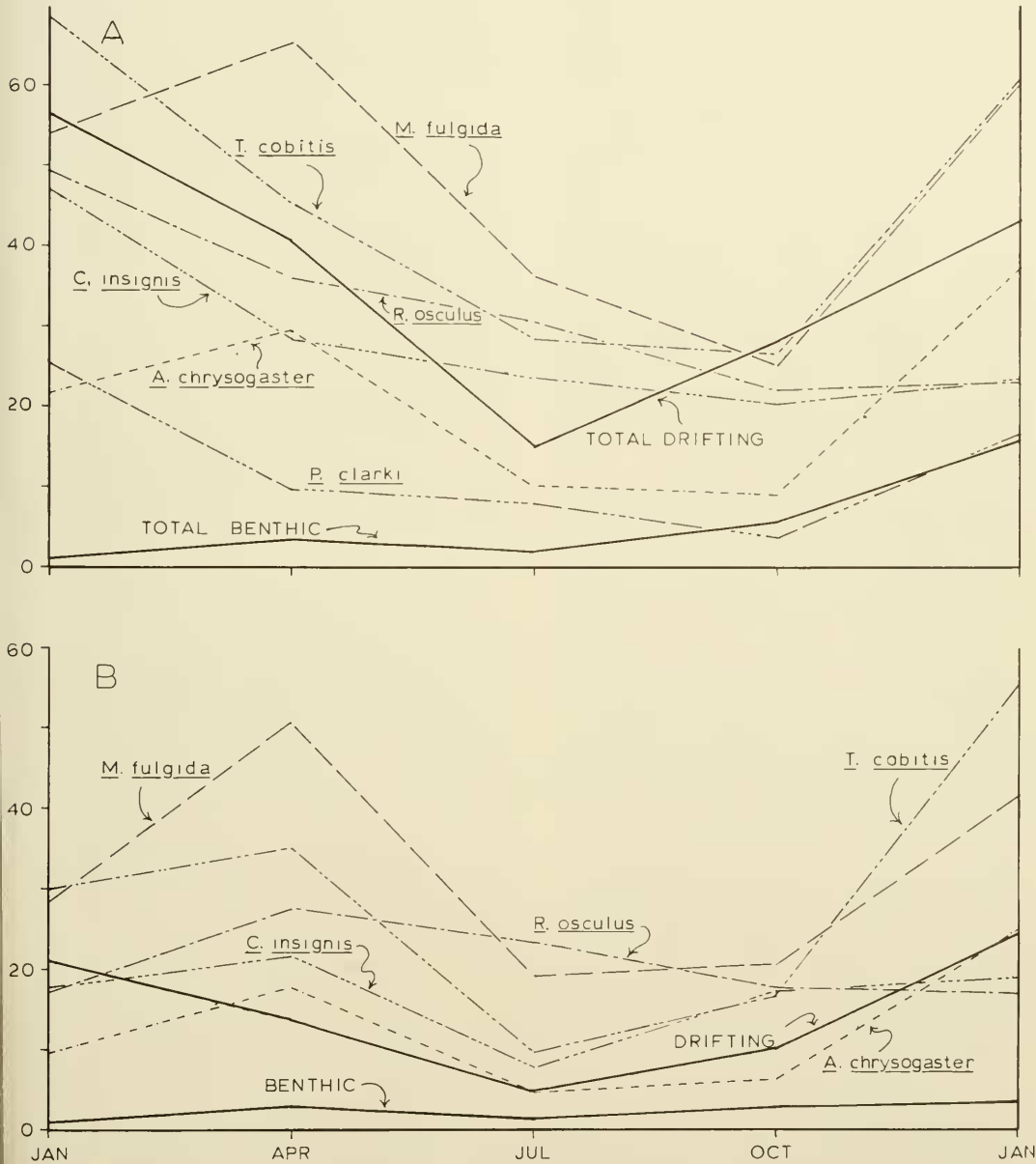


Fig. 4. Total weights of drift (mg/m³), benthos (g/m³), and percentages of total stomach volumes in six fish species for all invertebrate groups (A) and for ephemeropteran nymphs (B) from Aravaipa Creek, Arizona, 1975-1976.

mer floods in July, and benthic biomass also had declined at that time from the previous sampling period. Because mayfly nymphs dominated both benthos and drift, changes in Figure 4 result largely from adjustments in their population structure. Average weights of individual mayfly nymphs decreased in April, to remain low throughout summer as large numbers emerged and early instars were recruited into the populations. Small average sizes of baetid nymphs persisted through January 1976 in benthic samples, but a large standing crop was present and larger individuals appeared in drift (Table 8).

Preferential feeding on dipteran larvae by bottom-feeding fishes seemed indicated by data for April 1975 (Fig. 3). Dipteran larvae were relatively abundant in benthic samples at that time, although far less so than mayfly nymphs; yet they comprised a greater proportion of total stomach contents than mayflies in *Rhinichthys osculus*, *Tiaroga cobitis*, and *Catostomus insignis* (Tables 4-6, Fig. 4). Other fishes also ate substantial quantities of dipterans, but *Meda fulgida* and *Agosia chrysogaster* consumed mostly mayfly nymphs, and *Pantosteus clarki* fed heavily upon algae (Fig. 3). A relatively large year class of plecopteran nymphs also was present and was cropped by all fishes except *P. clarki*.

Each of the fishes, again excepting *P. clarki*, ate relatively greater amounts of ephemeropteran nymphs in April, perhaps exploiting the comparatively large, pre-emergence instars that were present.

Dramatic changes in stomach contents of almost all fishes occurred in July, coincident with declines in both dipteran larvae and

mayfly nymphs as a result of summer flooding (Bruns and Minckley 1980), and a substantial decrease in average individual sizes of the latter (Figs. 3-4; Table 8). Alterations in food habits consisted of a shift by 3 of the 6 fishes to different prey. Each alternate prey item increased in relative availability in July from the previous sampling period.

These changes reflected opportunistic feeding behavior of each fish species within its respective habitat. Spikedace increased its use of terrestrial organisms and winged aquatic insects, exploiting its mid- to surface water habit. A similar shift in food habits of this species was reported by Barber and Minckley (1982) in response to summer spates in Aravaipa Creek in 1966-67. Loach minnows preyed heavily upon rheophilic trichopteran larvae, in fact to a degree disproportionate to indicated abundance of that group (Fig. 3). A third fish, the Sonora sucker, amplified its cropping of bottom-inhabiting turbellarians that had commenced in April until the worms made up more than 40 percent of total stomach contents in July.

Diversification of diet was minimal in speckled dace, with a small increase in predation upon winged insects being the only apparent change in July. Perhaps this was a response to summer increases in abundance of that food source (Fig. 3). Desert suckers fed upon turbellarians, to the exclusion of other invertebrates, but this may reflect incidental intake of the abundant flatworms from riffle bottoms. Longfin dace persisted in feeding upon algae in July, along with a consistent ration of mayflies, and even showed a tendency toward eating fewer food groups in summer and autumn (Fig. 3).

TABLE 8. Mean weights of individual ephemeropteran nymphs, individual baetid ephemeropteran nymphs, and numbers of each per unit sample in benthos and drift from Aravaipa Creek, Arizona, 1975-1976.

Items	Jan	Apr	Jul	Oct	Jan
TOTAL EPHEMEROPTERA					
Benthos, wt. in mg	0.84	0.90	0.52	0.47	0.69
No/m ²	974	2,982	2,249	6,115	5,166
Drift, wt. in mg	1.58	0.58	0.51	0.44	1.00
No/m ³	13.30	25.10	9.00	22.40	22.30
BAETIDAE					
Benthos, wt. in mg	0.99	0.90	0.56	0.51	0.30
No/m ²	565	1,851	1,453	4,930	3,552
Drift, wt. in mg	1.73	0.50	0.34	0.62	1.00
No/m ³	8.40	15.70	6.70	14.90	19.20

Coincident with the return of abundant mayfly nymphs in October, average sizes of individual nymphs increased, alternate food organisms declined in abundance (in 2 instances of 3 recorded), and food habits of fishes shifted back to a pre-July condition. Dipteran larvae failed to increase to their former abundance, however, and were largely replaced in benthic biomass by trichopteran larvae. The fishes generally responded in turn, and trichopterans were consistently present in stomachs of all species except *P. clarki* in January 1976 (Fig. 3; Tables 1-7).

July percentages of total stomach volumes of all fishes decreased dramatically from April levels and remained relatively low through October (Fig. 4). Indicated availability of drift decreased in July and increased in October; benthos varied little from April through October. These declines in apparent food intake in summer and autumn may reflect physiological states of the fishes, induced by high summer temperatures, reduced reproductive activity, or other factors, as well as a change in the food base. It also may be a result of faster digestive rates (more rapid evacuation of the stomach) at higher temperatures.

SUMMARY AND CONCLUSIONS

Native fishes in Aravaipa Creek, Arizona, cropped foods relative to abundance of those foods within the system. Most fishes, excepting the single herbivore and a facultative omnivore, fed upon the same staple items, ephemeropteran nymphs, and secondarily upon trichopteran or dipteran larvae, or winged insects. The herbivore took animal foods when an item was abundant, and the omnivorous species ate almost as many nymphal mayflies, on the average, as did the carnivorous forms, but apparently selected against other invertebrates.

The degree to which diets of fishes resemble one another in a given system may have pronounced effects upon their feeding characteristics (Kawanabe 1959, Keast 1966). At times when foods are plentiful, direct effects of broad overlap in diets may be negligible. However, when foods are scarce, fishes with the greatest similarity in diet will face

increased interspecific interactions (Starrett 1950, Zaret and Rand 1971). Competition will be most severe for those species having narrow or inflexible feeding habitats (Kawanabe 1959).

Abundance of invertebrate foods in Aravaipa Creek, coupled with marked spatial partitioning of habitat by fishes present, seemed to preclude severe interspecific interactions for food. Even species with limited food habits and feeding repertoire, for example *Tiaroga cobitis*, which ate only 11 of 75 items considered available and was essentially monophagic during 4 of 5 sampling periods, seemed to have little difficulty in shifting to an alternate food source when mayflies became less abundant. Decreased total food volumes in all stomachs in July, when the major shifts in food habits occurred, may have related to decreased food supply. Stomachs remained relatively empty in October after benthos and drift increased, and shifts from alternate food supplies back to ephemeropteran nymphs had also occurred.

Mendelson (1975) similarly found that standing crops of fish food organisms appeared sufficient in Roxbury Creek, Wisconsin, to support larger fish populations than were actually present. Starrett (1950) observed that food was not an obvious limiting factor for several species of minnows in the Des Moines River, Iowa. All were able to draw from a common food base with little or no apparent competition. If direct competition for food were a significant factor in these systems, greater divergence in diets might be expected (Lawlor and Smith 1976). In situations where little partitioning of food supply by fishes appears to occur, such as in Aravaipa Creek, opportunism appears a common tendency (Mendelson 1975, Keast 1966). When a staple food decreases in abundance, a shift occurs to another locally or seasonally abundant item. Some fishes continued to feed generally upon the same foods throughout the year; others shift, each of the last to a different alternate prey. The shift by this last group of fishes implies a sophisticated spatial and behavioral adjustment that allows exploitation of an existing food base without increasing interspecific feeding interactions.

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